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First macrobiota biomineralisation was environmentally triggered

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Abstract

Why large and diverse skeletons first appeared ca. 550 million years ago is not well understood. Many Ediacaran skeletal biota show evidence of flexibility, and bear notably thin skeletal walls with simple, non-hierarchical microstructures of either aragonite or high-Mg calcite. We present evidence that the earliest skeletal macrobiota, found only in carbonate rocks, had close soft-bodied counterparts hosted in contemporary clastic rocks. This includes the calcareous discoidal fossil *Suvorovella,* similar to holdfasts of Ediacaran Biota taxa previously known only as casts and moulds, as well as tubular and vase-shaped fossils. In sum these probably represent taxa of diverse affinity including unicellular eukaryotes, total group cnidarians, and problematica.

Our findings support the assertion that the calcification was an independent and derived feature that appeared in diverse groups where an organic scaffold was the primitive character, which provided the framework for interactions between extracellular matrix and mineral ions. We conclude that such skeletons may have been acquired with relative ease in the highly saturated, high

alkalinity carbonate settings of the Ediacaran, where carbonate polymorph was further controlled by seawater chemistry.

The trigger for Ediacaran biomineralisation may have been either changing seawater Mg/Ca and/or increasing oxygen levels. By the early Cambrian, however, biomineralisation styles and the range of biominerals had significantly diversified, perhaps as an escalating defensive response to increasing predation pressure. Indeed skeletal hardparts had appeared in clastic settings by Cambrian Stage 1, suggesting independence from ambient seawater chemistry where genetic and molecular mechanisms controlled biomineralisation and mineralogy had become evolutionarily constrained.

Keywords: Ediacaran; Biomineralisation; Macrobiota; Metazoans; Carbonate supersaturation

1. Introduction

Sizable calcareous skeletons (1 mm to 1 m) appeared rapidly and globally in the late Ediacaran, ca. 550 Ma (1), marking a step change in the workings of the carbon cycle and marine ecosystem complexity. Many modern metazoan groups with skeletal taxa have non-skeletal close relatives, and early Cambrian skeletal taxa of varied mineralogy represent a diverse range of phyla (2). These observations support the hypothesis of convergent or parallel evolution of biomineralisation at the phylum level (2), suggesting the operation of an extrinsic trigger in the Ediacaran-early Cambrian that in turn conferred selective advantage to the acquisition of a skeleton.

The earliest skeletal macrobiota appeared in redox stratified oceans often characterised by a shallow and fluctuating oxic chemocline (3,4). Possible triggers for biomineralisation include the availability of oxygen, changes in seawater chemistry such as an increase in calcium, or the rise of predation (5). Much uncertainty persists, however, as to the relative importance of these factors, or their potential inter-relationships.

Orthologous genes and their encoded proteins involved in biomineralisation are known to have been co-opted and diversified among vertebrates, echinoderms, molluscs, and bilaterians in general

(6,7). Multiple origins for biomineralisation in animals is supported by the appearance of biomineralisation after divergence of the major bilaterian clades, and also by the observation that some Cambrian skeletal taxa are resolved as early members of extant phyla rather than stem representatives of larger groups such as Deuterostomia, Protostomia, Bilateria or even Metazoa (2).

New data show that the stratigraphic distribution of so-called Ediacaran and earliest Cambrian skeletal biotas overlap without notable biotic turnover, and hence do not support the contention that mass extinction of the Ediacaran biota facilitated the Cambrian radiation (8). The relationship between Ediacaran and early Cambrian skeletal taxa remains, however, unclear.

Here we consider the nature of the earliest (Ediacaran) macrofossil biomineralisation, provide evidence that some of the oldest known skeletal macrobiota have almost morphologically identical soft-bodied counterparts, and finally propose that highly supersaturated and high alkalinity carbonate oxygenated settings promoted early biomineralisation. We further highlight broad differences between dominant Ediacaran and early Cambrian macrobiota biomineralisation styles.

2. The nature of the earliest macrofossil biomineralisation

Most skeletons combine minerals with structural organic matter, where the physiological cost of producing the mineral is generally small compared to the organic matrix (9). Several features of Ediacaran skeletal macrofossils suggest the operation of relatively simple biomineralisation mechanisms from a pre-existing organic matrix.

Some tubular skeletal biota show evidence of flexibility suggesting the presence of relatively elastic organic skeleton impregnated with mineral granules (10). In these forms, the primary wall is also often extremely thin: <60 μm in *Cloudina* (10), <90 μm in *Sinotubulites* (11-13), and < 40 μm in *Suvorovella* (below). Such skeletal microstructures are also simple, homogenous, with no documented retention of preferred crystallographic orientation, and often resemble abiotic cement crusts. Many are either fibrous or microgranular (which may represent diagenetic recrystallization of a primary fibrous microstructure), where individual crystallites are not composed of smaller

units, i.e. they are non-hierarchical.

All known Ediacaran skeletal biota produced either aragonite or high-Mg calcite: carbonate polymorphs interpreted to have been favoured by ambient seawater chemistry (14). Indeed all known Ediacaran skeletal taxa were immobile benthos found exclusively in shallow marine carbonate settings (15). Finally, we note that Ediacaran skeletal taxa are of diverse affinity, and some possessed a non-mineralised, organic, counterpart, as detailed below.

3. Contemporary skeletal and non-skeletal counterparts

Here we document examples of the four contemporary skeletal and non-skeletal taxonomic pairs: *Suvorovella-Eoporpita; Cloudina-Conotubus*; *Sinotubulites-Corumbella*, and *Protolagena-Sicylagena*.

The discoidal skeletal *Suvorovella* (Figs. 1; 2a) occurs in carbonates of the Aim Formation of the south-eastern Siberian Platform (16,17), ca 550-543 Ma. Whole *Suvorovella* shells and broken angular fragments form a thick and persistent shell bed from 1.5 to 2.3 m in thickness, which extends to over 1 km in length, often cross-bedded with coated grains including microbial oncoids (Fig. 1d). *Suvorovella* ranges from 10 to 100 mm in diameter and consists of a hollow, flattened disc, with a low conical, slightly eccentrically positioned, an irregularly concentrically folded apex, and an outer flat zone bearing widely separated thin concentric ribs and radiating low relief ridges imparting a diamond-shaped pattern to the surface (Figs. 1a and b; 2a). These radiating ridges are probably casts of thin, densely anastomosing grooves running from the apex to the periphery, terminating in a distinct rim (Figs. 1a and b). The lower surface of the shell is smooth.

Suvorovella specimens are preserved as replicas by an isopachous crust of early diagenetic marine radial fibrous dolomite cement that precipitated upon a micritic envelope (4) (Figs. 1e and g). Precipitation of such cements required a rigid template capable of preserving fine scale morphological features. The original shell was probably aragonitic, which was replaced by dolomitising waters during transgression (4).

Suvorovella has a similar size range and close overall morphology to many discoidal, soft-bodied Ediacaran taxa (18-20). But these by contrast show stretching, folding, and other plastic deformations, and are always preserved as casts and moulds (18). In particular, the soft-bodied taxa *Eoporpita medusa* (Fig. 2e), *Hiemalora stellaris*, and *Palaeophragmodictya spinosa* show both a similar low conical, eccentrically positioned, folded apex, and a flatter outer zone with dense radiating branching structures similar to *Suvorovella* (19,20).

In *Suvorovella* shells, the very tip of the apex is never preserved, suggesting that the disc may have connected to a non-skeletal structure such as a stem, tube, tentaculate structure or cone as found in soft-bodied Ediacaran taxa. Of note is that the discoidal soft-bodied taxon *Aspidella* is found in the sandstones of the Aim Formation (17), within the same sequence immediately underlying the carbonate units that contain *Suvorovella* (4). Such discs have been interpreted as holdfasts of taxa of unknown affinity, orientated in life by attachment of the apex to, or within, sea floor sediment (18-20). We hence tentatively suggest a similar function for *Suvorovella* (Fig. 1c**)**.

The globally-distributed *Cloudina* (ca. 550-540 Ma) forms a tube of nested funnel-shaped and eccentrically arranged cones with flaring rims, up to 150 mm long and 7 mm in diameter (Fig. 2b). The *Cloudina* skeleton is composed of extremely thin (8-12 μm) primary layers of elongated micritic crystals (< 4 μm) fusing to form secondary lamina (up to 60 μm thick), strengthened by early epitaxial cement crusts which infill the space between walls of successive cones (10, 11, 21). The non-skeletal *Conotubus* (Fig. 2f) shows a very similar morphology and size range (22,23). *Conotubus* occurs just below *Cloudina* in the same sections of the Dengying Formation on the Yangtze Platform, China, with *Conotubus* restricted to siltstones while *Cloudina* is confined to overlying carbonates (22). *Cloudina* shows evidence for asexual reproduction including intercalar budding and longitudinal fission. These reproduction styles as well as rapid increase of the tube diameter, a closed apex, occasional tabulae and hexagonal symmetry of some species, are compatible with a total group cnidarian and, therefore, a crown-eumetazoan affinity (11, 21).

The skeletal *Sinotubulites* (Fig. 2c) also occurs in the Dengying Formation, as well as Western Laurentia (Mexico and USA), and Spain (11-13). *Sinotubulites* possesses a semi-circular to polygonal open thick tube up to 20 mm in length and 4-5 mm in diameter, with multiple, fine concentric slightly eccentric layers (40-50 μm thick) of micritic texture; these are transversely and unevenly corrugated to form incomplete ringlets on the surface merging into each other along the tube length. The organic-walled *Corumbella* known from upper Ediacaran clastics of South America and Western Laurentia (24,25), resembles *Sinotubulites* in all fine-scaled detail, including multiple concentric layers, the surface pattern of merging ringlets, and a polygonal cross section (Fig. 2g). Similar alternating 'plates' are present in both *Corumbella* and *Sinotubulites*, arranged in a slightly asymmetrical pattern along the mid-line of the fossils. In the soft-bodied *Corumbella* these structures resemble 'plates' (Fig. 2g), while in skeletal *Sinotubulites* these structures possess a 3D form and hence have a facet-like appearance (Fig. 2c). *Corumbella* is slightly longer (up to 34 mm) than the maximum size noted *Sinotubulites,* but all documented specimens of the latter are incomplete fragments. In the Tamengo Formation, Brazil, *Corumbella* occurs within shale units which are overlain by carbonates containing *Cloudina waldei,* which is morphologically more similar to *Sinotubulites* rather than to any other *Cloudina* species (13). The morphological features of *Corumbella* are consistent with a total-group cnidarian affinity, but the affinity of *Sinotubulites* is problematic.

Finally, the vase-shaped problematic skeletal taxa *Protolagena* (Fig. 2d) from the Dengying Formation, is up to 2.4 mm in diameter with a flaring aperture and a thin (14-40 μm) multi-layered, micritic calcareous wall (26). It is only mineralisation that allows this taxon to be distinguished from its organic-walled counterpart *Sicylagena* (Fig. 2h), which is restricted to the clastic beds of the same formation (26). *Protolagena* and *Sicylagena* may represent non-metazoan unicellular eukaryotes (protists).

Whilst it is possible that these skeletal/non-skeletal pairs are taphonomic or diagenetic variants of the same taxa, or different taxa restricted to specific ecological niches or environmental settings, we argue that this is not supported by further observations of differences in preservational style.

Suvorovella, compared to discoidal taxa such as *Aspidella, Eoporpita, Hiemalora*, and *Palaeophragmodictya'* is preserved as fossils of notably different original rigidity, and the existence of primary biomineralized shells in *Suvorovella* is confirmed by the presence of multiple broken, angular fragments forming a shell hash (Fig. 1d). Such a depostional style has never been observed in localities yielding soft-bodied Ediacara biota. In addition, *Suvorovella* specimens never present features of plastic deformation such as stretching, wrinkling, folding, contraction, or other post-mortem degradational features as noted in soft-bodied discoidal taxa (18). Even when preserved in carbonates, such as in the Khorbusuonka Formation, northern Siberian Platform, *Aspidella, Mawsonites,* and *Hiemalora* lack petrographic evidence for dissolution of original skeletal material (27).

Likewise, *Corumbella,* when preserved in the carbonate Tagatia Guazu Formation of Paraguay shows no petrographic evidence for the presence of any original skeletal hardparts (28). Indeed, here *Corumbella* still shows features of plastic deformations such as bending, twisting and axial-stretching without any loss of overall integrity (24, 25). *Conotubus* also shows similar bending, folding, and transverse segment imbrication (23). Even when ruptured, *Corumbella* shows irregular tears rather than an angular breakage (24). Such preservation is in notable contrast to the tubes of *Cloudina* which, like *Suvorovella,* can show brittle breakage and form concentrated shell beds (29). *Cloudina* can also show both elevated growth of cemented and mutually-attached individuals to form substantial reef frameworks (30, 31), and possible evidence of predatory boring (32).

Finally, it might be argued that these pairs are merely similar as a consequence of their simplicity of form. But shared, fine-scale features suggest they are indeed the same, or closely-related, taxa. Moreover these Ediacaran skeletal fossils are no simpler than any Cambrian metazoans of the poriferan-cnidarian grade, and each has a unique construction. The *Cloudina* tube is built of

eccentrically nested funnel-like elements with flaring upper margins, and the *Sinotubulites* tube is polygonal in cross section and consists of concentric nested tubicolous elements with similar alternating plates or facets arranged asymmetrically along the mid-line. The outer tube surface also has a pattern of incomplete ringlets separated by longitudinal ridges (12,13). *Suvorovella* is a hollow disc-like shell with two distinct zones on the upper shell, namely a low conical, eccentrically positioned and tightly concentrically folded apex, and an outer flat zone bearing widely separated thin concentric ribs and braided ridges imparting a diamond-shaped pattern to the surface. Except for the soft-bodied twins of these fossils, no other known Ediacaran or Cambrian fossils share these features.

All described taxa are either of unresolved affinity, unicellular eukaryotes (protists), or possible total group cnidarian affinity (crown-eumetazoans). The affinities of *Sinotubulites* and *Suvorovella* are unconstrained but their overall skeletal structures are more complex than known in unicellular testate organisms and are incompatible with the organisation of calcified algae.

4. Implications for the origins of biomineralisation pathways

Calcareous organisms synthesize calcium-binding and extracellular matrix proteins that provide templates for mineralisation as well as macromolecules to act as anti-calcifying inhibitors, so essentially placing diagenetic crystal growth under biological regulation (1, 33, 34). This suggests that such biomineralisation probably originated from a calcium-regulated extracellular matrix system (33,34).

Our findings support the assertion that the calcification process might be a derived feature in many groups where chitin, collagen or other organic matrices localized in epithelial cells may be the primitive character predating biomineralisation: organic scaffolds provided the framework for interactions between extracellular matrix and mineral ions (35). Indeed we note that calcium signalling pathways underwent a dramatic and unparalleled diversification coincident with the radiation of animals (36).

5. The role of high carbonate supersaturation

Ediacaran skeletal taxa are immobile but of diverse affinity: problematic macrobiota, possible total group Cnidaria, as well as unicellular eukaryotes. Prior to the late Ediacaran, most microfossils (inferred to be unicellular eukaryotes), despite varied probable affinities, possessed either organic or agglutinated tests only (37) with the exception of phosphatic microfossils of probable algal affinity in the mid-Proterozoic (38).

All Ediacaran calcareous taxa are found only in carbonate rocks, but have soft-bodied counterparts that occur mainly in clastic rocks, often within the same conformable sequences. This observation suggests the operation of local environmental conditions that promoted calcareous skeletonisation in pre-existing soft-bodied biota of diverse affinity but with relatively low metabolic demands.

We propose that the Ediacaran macrobiota biomineralisation, including the first possible metazoan calcification, was facilitated by the high carbonate supersaturation and alkalinity of Ediacaran shallow marine carbonate settings. Experimentation confirms that modern carbonate skeleton formation is strongly dependent on carbonate supersaturation (39), and so calcification has a relatively low metabolic cost in the highly saturated surface seawaters of low latitudes. For example, despite divergent skeletal morphologies (1), calcium carbonate skeletons may have appeared at least twenty times among metazoans and as many as eight times within both the Porifera and Cnidaria alone (40).

The influence of unusual seawater chemistry during this interval is further supported by examples of anomalously large carbonate skeletons, grains, and structures that exceed Cambrian equivalents by one to two orders of magnitude: 1) The skeletal taxa *Namapokia* in the Nama Group, Namibia, which reaches diameters of over 1 m (41), 2) Densely aggregating metazoan reefs with volumetrically significant syn-sedimentary cement >10 m in width (31), 3) *Suvorovella* shell beds ca.1 km length, and 4) Widespread distribution of giant aragonite and high-Mg calcite ooids

(42). Generally high alkalinity is also consistent with both the global dominance of carbonate lithologies in terminal Ediacaran successions (43) and the extremely high estimated carbonate sediment accumulation rates for this interval, e.g. >650 m/ca.10 Myr for the Dengying Formation (23), and >1000 m/ca.10 Myr for the Nama Group (43).

6. Discussion

Despite the first appearance of stalked, frondose macrobiota at ca.578 Ma and soft-bodied tubular forms at ca.550 Ma, no large biomineralised taxa are known until the terminal Ediacaran (ca.550 Ma). That diverse skeletal taxa appear broadly synchronously supports the hypothesis of a terminal Ediacaran environmentally-driven biocalcification event.

But while locally high carbonate supersaturation appears to have facilitated calcareous skeltonisation, globally high supersaturation long predated the appearance of macrobiota hardparts. Archean and Proterozoic seawater is thought to have been highly supersaturated with respect to carbonate, exceeding that of modern oceans (43): saturation alone was therefore sufficient to alleviate any metabolic barriers on carbonate biomineralisation. This suggests that factors other than changes in seawater carbonate saturation provided a broadly synchronous and global trigger for late Ediacaran biomineralisation.

One possibility is that the progressive lowering of seawater Mg/Ca by increased the input of Ca into oceans, may have caused the demise of 'aragonite-dolomite' seas so ushering-in an interval of 'aragonite seas' (4). A further, and perhaps related control, is rising oxygenation. Although modern soft-bodied sponge grade animals may tolerate oxygen concentrations as low as 1.25–10 mM (44), skeletonisation is hypothesised to have required higher levels of oxygen, > 13 mM (45), perhaps in part due to the relatively high energetic cost of structural collagen formation and complex skeletal microstructures (46). The relatively high oxygen requirements of Ediacaran skeletal biota have been confirmed by the identification of low-oxygen, manganous water column conditions in intervals of Ediacaran successions that lack skeletal taxa (47).

The observations presented here support predictions as to the presence of diverse, pre-existing soft-bodied representatives prior to the acquisition of calcareous skeletons, and that the first macrobiota capable of first utilizing increased oxygen for extensive collagen fibrogenesis would likely be those with the lowest metabolic demands, in particular those without advanced circulatory-respiratory systems (46). It has been hypothesised that induced biologically-mediated calcification was an attempt to detoxify excess calcium ions (48), or the molecular inhibitors required as anti-calcification defences in soft-bodied ancestors might have been recruited for control over skeleton growth (34). It is possible that rising oxygen levels may, however, have been necessary to fuel the co-optive selection of proteins from a pre-adaptive state to allow an adaptive breakthrough (46).

Understanding the degree of biological control over Ediacaran macrobiota biomineralisation is critical. Biologically-induced precipitates form as a result of metabolic activities that affect pH, pCO_2, and secretion products where the cell is a causative agent only with no control over mineral type or habit (9, 49). By contrast, in biologically-controlled systems, cellular processes direct the nucleation, growth, morphology and final location of precipitated minerals. Almost all controlled mineralization processes occur in an isolated biological environment, although the degree of control varies considerably. A potentially widespread biomineralisation process also involves a transient amorphous calcium carbonate (ACC) precursor phase formed from a highly saturated solution with additions such as Mg or certain proteins that prevent crystallisation (49). Elemental compositional or microstructural heterogeneity is the mark of biologically-induced minerals, as the form biominerals resulting from induced processes vary according to the environmental settings in which they form (9,49). Analysis of individual crystal shapes and the stability of faces expressed can also inform the mechanisms of controlled growth, as can the nature of any biologically-controlled chemical and isotopic composition (vital effects).

Many, but not all, Ediacaran macrobiota skeletal microstructures are either microgranular or fibrous, with a non-hierarchical organisation. This perhaps suggests the operation of biomineralisation mechanisms that were not under tight biological control. Indeed we note that the

only biomineralised Ediacaran macrobiota to lack a non-mineralised twin possessed more advanced skeletal microstructures constructed of either multiple layers or several different fabrics, with a hierarchical organisation where each fabric has specific crystallites composed of sub-units similar to those known in earliest Cambrian skeletal metazoans (11). But a detailed understanding of Ediacaran biomineralisation processes is problematic, as evidence for environmentally-induced heterogeneity, the potential role of ACC, original crystal shape and preferred crystal orientation, and the presence of vital effects is difficult to establish given the diagenetic replacement of originally aragonitic or high Mg calcite skeletons and the unknown structure of the organic matrix.

A change in the ecological landscape further created by the rise of predation would have placed a premium on the acquisition of protective hardparts (1). The early Cambrian record shows a rapid increase in both diversity of mineralogy and complexity of skeletal microstructures which become conserved within lineages, suggesting that while calcification may first have arisen as a non-selective response to environmental change, it was later co-opted for defence and subsequently evolved under tighter biological control. Indeed we note also that skeletal hard parts first appeared in clastic environments in Cambrian Stage 1, suggesting independence from ambient sea water chemistry. By the early Cambrian genetic and molecular mechanisms may have controlled biomineralisation and mineralogy had become evolutionarily constrained (2).

7. Conclusions

We report that the oldest known skeletal macrobiota (ca.550 Ma), including unicellular eukaryotes and possible metazoans, found in carbonate settings, have almost morphologically identical soft-bodied counterparts often found in the clastic horizons of the same contemporary stratigraphic sequences. These forms are diverse, and include tubular and vase-shaped taxa, as well as the first example of a skeletonised discoidal fossil, possibly a holdfast, of Ediacaran Biota. In sum they represent problematic macrobiota, possible total group Cnidaria, as well as unicellular

eukaryotes. Skeletal microstructures are either microgranular or fibrous, with non-hierarchical organsiation.

We conclude that the macrobiota biomineralisation was first facilitated by the high carbonate saturation of Ediacaran seawater in local shallow, carbonate settings, and that such calcification was potentially under limited biological control in sessile taxa that probably required only modest modification of pre-existing organic templates.

The first appearance of large skeletal taxa may have been facilitated by changing seawater Mg/Ca and/or rise of oxygen. We hypothesise that from Ediacaran beginnings, macrobiota biomineralisation diversified in complexity and had become under tighter biological control by the early Cambrian, including occupation of clastic environments suggesting independence from ambient seawater chemistry, probably fuelled by an escalating defensive response to increasing predation pressure and other feedbacks.

Metazoans probably originated in the Cryogenian, diversified in the Neoproterozoic, and came to ecological dominance in the Cambrian. But molecular clock estimates predict the existence of only stem members of extant phyla in the late Ediacaran, with crown groups of most animal phyla originating in the Cambrian (50). Complex hierarchical Cambrian skeletal fabrics are notably different from the extremely thin, simple, Ediacaran skeletal organisations and represent a more advanced step in the evolution of biomineralisation.

Our findings support recent molecular evidence that the first appearance of fossil skeletons faithfully reflects their independent origins and further suggests that developmental and molecular architecture for biomineralisation evolved prior to the divergence of the metazoan phyla, providing a mechanism for synchronous, multiple origins of biomineralisation through exaptation of existing genes (2). This is also compatible with the assertion that the ‘Cambrian Explosion’ is a biological signal of the diversification of preservable skeletal fossils, not of animals.

Ethics statement

This work has not involved any living subjects and conforms to the Ethics guidelines of the School of GeoSciences, University of Edinburgh.

Data accessibility

All data utilised in this study are presented in the text.

Author contributions

RW and AZ designed the study; AI re-found the original *Suvorovella* fieldsite, undertook initial fieldwork, and collected most material. AI and AZ carried out the morphological description, undertook SEM analysis and reconstructed *Suvorovella*; RW undertook the petrographic analysis of *Suvorovella;* RW and AZ drafted the manuscript; All authors gave final approval for publication.

Competing interests

We have no competing interests

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Figure captions

Fig. 1. *Suvorovella aldanica* Vologdin and Maslov, 1960, Aim Formation, Ediacaran; Siberian Platform, Republic of Sakha (Yakutia), Russia. (A) Detail of shell inner lower surface showing outer flat zone with diamond-shaped pattern and concentrically arranged chambers. **(B)** Detail of shell showing folded apex and outer flat zone with diamond-shaped pattern, latex mould of inner lower surface, PIN no. 5119/1063. **(C)** Reconstruction, diameter 100 mm. **(D)** Field photograph of shell bed of whole and broken *Suvorovella* shells. **(E)** Photomicrograph of thin section showing micritic envelopes (arrowed) around *Suvorovella*, encrusted by an isopachous crust of early diagenetic radial fibrous dolomite cement. **(F)** SEM image of detail of outer upper surface of shell at the apex showing concentric ribs and uneven surface. **(G)** SEM image of broken shell edge showing micrite envelope (M) encrusted by early marine radial fibrous dolomite cement (D). Specimens figured in A, B, F and G are housed in Palaeontological Institute named after A.A. Borisyak, Russian Academy of Sciences, Moscow (PIN).

Fig. 2. Ediacaran skeletal (A-D) and non-skeletal (E-H) counterparts. (A) Skeletal *Suvorovella*;. **(B)** Skeletal *Cloudina* (Photo: Shuhai Xiao). **(C)** Skeletal *Sinotubulites* (Photo: Shuhai Xiao/Yaoping Cai). **(D)** Skeletal *Protolagena* (Photo: Shuhai Xiao/Hong Hua). **(E)** Organic *Eoporpita medusa*. **(F)** Organic *Conotubus* (photo: James Schiffbauer/Yaoping Cai). **(G)** Organic *Corumbella* (photo: Lucas Warren). **(H)** Organic *Sicylagena* (Photo: Shuhai Xiao/Hong Hua).

First macrobiota biomineralisation was environmentally triggered

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Abstract

Why large and diverse skeletons first appeared ca. 550 million years ago is not well understood. Many Ediacaran skeletal biota show evidence of flexibility, and bear notably thin skeletal walls with simple, non-hierarchical microstructures of either aragonite or high-Mg calcite. We present evidence that the earliest skeletal macrobiota, found only in carbonate rocks, had close soft-bodied counterparts hosted in contemporary clastic rocks. This includes the calcareous discoidal fossil *Suvorovella,* similar to holdfasts of Ediacaran Biota taxa previously known only as casts and moulds, as well as tubular and vase-shaped fossils. In sum these probably represent taxa of diverse affinity including unicellular eukaryotes, total group cnidarians, and problematica.

Our findings support the assertion that the calcification was an independent and derived feature that appeared in diverse groups where an organic scaffold was the primitive character, which provided the framework for interactions between extracellular matrix and mineral ions. We conclude that such skeletons may have been acquired with relative ease in the highly saturated, high

alkalinity carbonate settings of the Ediacaran, where carbonate polymorph was further controlled by seawater chemistry.

The trigger for Ediacaran biomineralisation may have been either changing seawater Mg/Ca and/or increasing oxygen levels. By the early Cambrian, however, biomineralisation styles and the range of biominerals had significantly diversified, perhaps as an escalating defensive response to increasing predation pressure. Indeed skeletal hardparts had appeared in clastic settings by Cambrian Stage 1, suggesting independence from ambient seawater chemistry where genetic and molecular mechanisms controlled biomineralisation and mineralogy had become evolutionarily constrained.

Keywords: Ediacaran; Biomineralisation; Macrobiota; Metazoans; Carbonate supersaturation

1. **Introduction**

Sizable calcareous skeletons (1 mm to 1 m) appeared rapidly and globally in the late Ediacaran, ca. 550 Ma (1), marking a step change in the workings of the carbon cycle and marine ecosystem complexity. Many modern metazoan groups with skeletal taxa have non-skeletal close relatives, and early Cambrian skeletal taxa of varied mineralogy represent a diverse range of phyla (2). These observations support the hypothesis of convergent or parallel evolution of biomineralisation at the phylum level (2), suggesting the operation of an extrinsic trigger in the Ediacaran-early Cambrian that in turn conferred selective advantage to the acquisition of a skeleton.

The earliest skeletal macrobiota appeared in redox stratified oceans often characterised by a shallow and fluctuating oxic chemocline (3,4). Possible triggers for biomineralisation include the availability of oxygen, changes in seawater chemistry such as an increase in calcium, or the rise of predation (5). Much uncertainty persists, however, as to the relative importance of these factors, or their potential inter-relationships.

Orthologous genes and their encoded proteins involved in biomineralisation are known to have been co-opted and diversified among vertebrates, echinoderms, molluscs, and bilaterians in general

(6,7). Multiple origins for biomineralisation in animals is supported by the appearance of biomineralisation after divergence of the major bilaterian clades, and also by the observation that some Cambrian skeletal taxa are resolved as early members of extant phyla rather than stem representatives of larger groups such as Deuterostomia, Protostomia, Bilateria or even Metazoa (2).

New data show that the stratigraphic distribution of so-called Ediacaran and earliest Cambrian skeletal biotas overlap without notable biotic turnover, and hence do not support the contention that mass extinction of the Ediacaran biota facilitated the Cambrian radiation (8). The relationship between Ediacaran and early Cambrian skeletal taxa remains, however, unclear.

Here we consider the nature of the earliest (Ediacaran) macrofossil biomineralisation, provide evidence that some of the oldest known skeletal macrobiota have almost morphologically identical soft-bodied counterparts, and finally propose that highly supersaturated and high alkalinity carbonate oxygenated settings promoted early biomineralisation. We further highlight broad differences between dominant Ediacaran and early Cambrian macrobiota biomineralisation styles.

2. The nature of the earliest macrofossil biomineralisation

Most skeletons combine minerals with structural organic matter, where the physiological cost of producing the mineral is generally small compared to the organic matrix (9). Several features of Ediacaran skeletal macrofossils suggest the operation of relatively simple biomineralisation mechanisms from a pre-existing organic matrix.

Some tubular skeletal biota show evidence of flexibility suggesting the presence of relatively elastic organic skeleton impregnated with mineral granules (10). In these forms, the primary wall is also often extremely thin: <60 μm in *Cloudina* (10), <90 μm in *Sinotubulites* (11-13), and < 40 μm in *Suvorovella* (below). Such skeletal microstructures are also simple, homogenous, with no documented retention of preferred crystallographic orientation, and often resemble abiotic cement crusts. Many are either fibrous or microgranular (which may represent diagenetic recrystallization of a primary fibrous microstructure), where individual crystallites are not composed of smaller

units, i.e. they are non-hierarchical.

All known Ediacaran skeletal biota produced either aragonite or high-Mg calcite: carbonate polymorphs interpreted to have been favoured by ambient seawater chemistry (14). Indeed all known Ediacaran skeletal taxa were immobile benthos found exclusively in shallow marine carbonate settings (15). Finally, we note that Ediacaran skeletal taxa are of diverse affinity, and some possessed a non-mineralised, organic, counterpart, as detailed below.

3. Contemporary skeletal and non-skeletal counterparts

Here we document examples of the four contemporary skeletal and non-skeletal taxonomic pairs: *Suvorovella-Eoporpita; Cloudina-Conotubus*; *Sinotubulites-Corumbella*, and *Protolagena-Sicylagena*.

The discoidal skeletal *Suvorovella* (Figs. 1; 2a) occurs in carbonates of the Aim Formation of the south-eastern Siberian Platform (16,17), ca 550-543 Ma. Whole *Suvorovella* shells and broken angular fragments form a thick and persistent shell bed from 1.5 to 2.3 m in thickness, which extends to over 1 km in length, often cross-bedded with coated grains including microbial oncoids (Fig. 1d). *Suvorovella* ranges from 10 to 100 mm in diameter and consists of a hollow, flattened disc, with a low conical, slightly eccentrically positioned, an irregularly concentrically folded apex, and an outer flat zone bearing widely separated thin concentric ribs and radiating low relief ridges imparting a diamond-shaped pattern to the surface (Figs. 1a and b; 2a). These radiating ridges are probably casts of thin, densely anastomosing grooves running from the apex to the periphery, terminating in a distinct rim (Figs. 1a and b). The lower surface of the shell is smooth.

Suvorovella specimens are preserved as replicas by an isopachous crust of early diagenetic marine radial fibrous dolomite cement that precipitated upon a micritic envelope (4) (Figs. 1e and g). Precipitation of such cements required a rigid template capable of preserving fine scale morphological features. The original shell was probably aragonitic, which was replaced by dolomitising waters during transgression (4).

Suvorovella has a similar size range and close overall morphology to many discoidal, soft-bodied Ediacaran taxa (18-20). But these by contrast show stretching, folding, and other plastic deformations, and are always preserved as casts and moulds (18). In particular, the soft-bodied taxa *Eoporpita medusa* (Fig. 2e), *Hiemalora stellaris*, and *Palaeophragmodictya spinosa* show both a similar low conical, eccentrically positioned, folded apex, and a flatter outer zone with dense radiating branching structures similar to *Suvorovella* (19,20).

In *Suvorovella* shells, the very tip of the apex is never preserved, suggesting that the disc may have connected to a non-skeletal structure such as a stem, tube, tentaculate structure or cone as found in soft-bodied Ediacaran taxa. Of note is that the discoidal soft-bodied taxon *Aspidella* is found in the sandstones of the Aim Formation (17), within the same sequence immediately underlying the carbonate units that contain *Suvorovella* (4). Such discs have been interpreted as holdfasts of taxa of unknown affinity, orientated in life by attachment of the apex to, or within, sea floor sediment (18-20). We hence tentatively suggest a similar function for *Suvorovella* (Fig. 1c**)**.

The globally-distributed *Cloudina* (ca. 550-540 Ma) forms a tube of nested funnel-shaped and eccentrically arranged cones with flaring rims, up to 150 mm long and 7 mm in diameter (Fig. 2b). The *Cloudina* skeleton is composed of extremely thin (8-12 μm) primary layers of elongated micritic crystals (< 4 μm) fusing to form secondary lamina (up to 60 μm thick), strengthened by early epitaxial cement crusts which infill the space between walls of successive cones (10, 11, 21). The non-skeletal *Conotubus* (Fig. 2f) shows a very similar morphology and size range (22,23). *Conotubus* occurs just below *Cloudina* in the same sections of the Dengying Formation on the Yangtze Platform, China, with *Conotubus* restricted to siltstones while *Cloudina* is confined to overlying carbonates (22). *Cloudina* shows evidence for asexual reproduction including intercalar budding and longitudinal fission. These reproduction styles as well as rapid increase of the tube diameter, a closed apex, occasional tabulae and hexagonal symmetry of some species, are compatible with a total group cnidarian and, therefore, a crown-eumetazoan affinity (11, 21).

The skeletal *Sinotubulites* (Fig. 2c) also occurs in the Dengying Formation, as well as Western Laurentia (Mexico and USA), and Spain (11-13). *Sinotubulites* possesses a semi-circular to polygonal open thick tube up to 20 mm in length and 4-5 mm in diameter, with multiple, fine concentric slightly eccentric layers (40-50 μm thick) of micritic texture; these are transversely and unevenly corrugated to form incomplete ringlets on the surface merging into each other along the tube length. The organic-walled *Corumbella* known from upper Ediacaran clastics of South America and Western Laurentia (24,25), resembles *Sinotubulites* in all fine-scaled detail, including multiple concentric layers, the surface pattern of merging ringlets, and a polygonal cross section (Fig. 2g). Similar alternating 'plates' are present in both *Corumbella* and *Sinotubulites*, arranged in a slightly asymmetrical pattern along the mid-line of the fossils. In the soft-bodied *Corumbella* these structures resemble 'plates' (Fig. 2g), while in skeletal *Sinotubulites* these structures possess a 3D form and hence have a facet-like appearance (Fig. 2c). *Corumbella* is slightly longer (up to 34 mm) than the maximum size noted *Sinotubulites,* but all documented specimens of the latter are incomplete fragments. In the Tamengo Formation, Brazil, *Corumbella* occurs within shale units which are overlain by carbonates containing *Cloudina waldei,* which is morphologically more similar to *Sinotubulites* rather than to any other *Cloudina* species (13). The morphological features of *Corumbella* are consistent with a total-group cnidarian affinity, but the affinity of *Sinotubulites* is problematic.

Finally, the vase-shaped problematic skeletal taxa *Protolagena* (Fig. 2d) from the Dengying Formation, is up to 2.4 mm in diameter with a flaring aperture and a thin (14-40 μm) multi-layered, micritic calcareous wall (26). It is only mineralisation that allows this taxon to be distinguished from its organic-walled counterpart *Sicylagena* (Fig. 2h), which is restricted to the clastic beds of the same formation (26). *Protolagena* and *Sicylagena* may represent non-metazoan unicellular eukaryotes (protists).

Whilst it is possible that these skeletal/non-skeletal pairs are taphonomic or diagenetic variants of the same taxa, or different taxa restricted to specific ecological niches or environmental settings, we argue that this is not supported by further observations of differences in preservational style.

Suvorovella, compared to discoidal taxa such as *Aspidella, Eoporpita, Hiemalora*, and *Palaeophragmodictya'* is preserved as fossils of notably different original rigidity, and the existence of primary biomineralized shells in *Suvorovella* is confirmed by the presence of multiple broken, angular fragments forming a shell hash (Fig. 1d). Such a depostional style has never been observed in localities yielding soft-bodied Ediacara biota. In addition, *Suvorovella* specimens never present features of plastic deformation such as stretching, wrinkling, folding, contraction, or other post-mortem degradational features as noted in soft-bodied discoidal taxa (18). Even when preserved in carbonates, such as in the Khorbusuonka Formation, northern Siberian Platform, *Aspidella, Mawsonites,* and *Hiemalora* lack petrographic evidence for dissolution of original skeletal material (27).

Likewise, *Corumbella,* when preserved in the carbonate Tagatia Guazu Formation of Paraguay shows no petrographic evidence for the presence of any original skeletal hardparts (28). Indeed, here *Corumbella* still shows features of plastic deformations such as bending, twisting and axial-stretching without any loss of overall integrity (24, 25). *Conotubus* also shows similar bending, folding, and transverse segment imbrication (23). Even when ruptured, *Corumbella* shows irregular tears rather than an angular breakage (24). Such preservation is in notable contrast to the tubes of *Cloudina* which, like *Suvorovella,* can show brittle breakage and form concentrated shell beds (29). *Cloudina* can also show both elevated growth of cemented and mutually-attached individuals to form substantial reef frameworks (30, 31), and possible evidence of predatory boring (32).

Finally, it might be argued that these pairs are merely similar as a consequence of their simplicity of form. But shared, fine-scale features suggest they are indeed the same, or closely-related, taxa. Moreover these Ediacaran skeletal fossils are no simpler than any Cambrian metazoans of the poriferan-cnidarian grade, and each has a unique construction. The *Cloudina* tube is built of

eccentrically nested funnel-like elements with flaring upper margins, and the *Sinotubulites* tube is polygonal in cross section and consists of concentric nested tubicolous elements with similar alternating plates or facets arranged asymmetrically along the mid-line. The outer tube surface also has a pattern of incomplete ringlets separated by longitudinal ridges (12,13). *Suvorovella* is a hollow disc-like shell with two distinct zones on the upper shell, namely a low conical, eccentrically positioned and tightly concentrically folded apex, and an outer flat zone bearing widely separated thin concentric ribs and braided ridges imparting a diamond-shaped pattern to the surface. Except for the soft-bodied twins of these fossils, no other known Ediacaran or Cambrian fossils share these features.

All described taxa are either of unresolved affinity, unicellular eukaryotes (protists), or possible total group cnidarian affinity (crown-eumetazoans). The affinities of *Sinotubulites* and *Suvorovella* are unconstrained but their overall skeletal structures are more complex than known in unicellular testate organisms and are incompatible with the organisation of calcified algae.

4. Implications for the origins of biomineralisation pathways

Calcareous organisms synthesize calcium-binding and extracellular matrix proteins that provide templates for mineralisation as well as macromolecules to act as anti-calcifying inhibitors, so essentially placing diagenetic crystal growth under biological regulation (1, 33, 34). This suggests that such biomineralisation probably originated from a calcium-regulated extracellular matrix system (33,34).

Our findings support the assertion that the calcification process might be a derived feature in many groups where chitin, collagen or other organic matrices localized in epithelial cells may be the primitive character predating biomineralisation: organic scaffolds provided the framework for interactions between extracellular matrix and mineral ions (35). Indeed we note that calcium signalling pathways underwent a dramatic and unparalleled diversification coincident with the radiation of animals (36).

5. The role of high carbonate supersaturation

Ediacaran skeletal taxa are immobile but of diverse affinity: problematic macrobiota, possible total group Cnidaria, as well as unicellular eukaryotes. Prior to the late Ediacaran, most microfossils (inferred to be unicellular eukaryotes), despite varied probable affinities, possessed either organic or agglutinated tests only (37) with the exception of phosphatic microfossils of probable algal affinity in the mid-Proterozoic (38).

All Ediacaran calcareous taxa are found only in carbonate rocks, but have soft-bodied counterparts that occur mainly in clastic rocks, often within the same conformable sequences. This observation suggests the operation of local environmental conditions that promoted calcareous skeletonisation in pre-existing soft-bodied biota of diverse affinity but with relatively low metabolic demands.

We propose that the Ediacaran macrobiota biomineralisation, including the first possible metazoan calcification, was facilitated by the high carbonate supersaturation and alkalinity of Ediacaran shallow marine carbonate settings. Experimentation confirms that modern carbonate skeleton formation is strongly dependent on carbonate supersaturation (39), and so calcification has a relatively low metabolic cost in the highly saturated surface seawaters of low latitudes. For example, despite divergent skeletal morphologies (1), calcium carbonate skeletons may have appeared at least twenty times among metazoans and as many as eight times within both the Porifera and Cnidaria alone (40).

The influence of unusual seawater chemistry during this interval is further supported by examples of anomalously large carbonate skeletons, grains, and structures that exceed Cambrian equivalents by one to two orders of magnitude: 1) The skeletal taxa *Namapokia* in the Nama Group, Namibia, which reaches diameters of over 1 m (41), 2) Densely aggregating metazoan reefs with volumetrically significant syn-sedimentary cement >10 m in width (31), 3) *Suvorovella* shell beds ca.1 km length, and 4) Widespread distribution of giant aragonite and high-Mg calcite ooids

(42). Generally high alkalinity is also consistent with both the global dominance of carbonate lithologies in terminal Ediacaran successions (43) and the extremely high estimated carbonate sediment accumulation rates for this interval, e.g. >650 m/ca.10 Myr for the Dengying Formation (23), and >1000 m/ca.10 Myr for the Nama Group (43).

6. Discussion

Despite the first appearance of stalked, frondose macrobiota at ca.578 Ma and soft-bodied tubular forms at ca.550 Ma, no large biomineralised taxa are known until the terminal Ediacaran (ca.550 Ma). That diverse skeletal taxa appear broadly synchronously supports the hypothesis of a terminal Ediacaran environmentally-driven biocalcification event.

But while locally high carbonate supersaturation appears to have facilitated calcareous skeltonisation, globally high supersaturation long predated the appearance of macrobiota hardparts. Archean and Proterozoic seawater is thought to have been highly supersaturated with respect to carbonate, exceeding that of modern oceans (43): saturation alone was therefore sufficient to alleviate any metabolic barriers on carbonate biomineralisation. This suggests that factors other than changes in seawater carbonate saturation provided a broadly synchronous and global trigger for late Ediacaran biomineralisation.

One possibility is that the progressive lowering of seawater Mg/Ca by increased the input of Ca into oceans, may have caused the demise of 'aragonite-dolomite' seas so ushering-in an interval of 'aragonite seas' (4). A further, and perhaps related control, is rising oxygenation. Although modern soft-bodied sponge grade animals may tolerate oxygen concentrations as low as 1.25–10 mM (44), skeletonisation is hypothesised to have required higher levels of oxygen, > 13 mM (45), perhaps in part due to the relatively high energetic cost of structural collagen formation and complex skeletal microstructures (46). The relatively high oxygen requirements of Ediacaran skeletal biota have been confirmed by the identification of low-oxygen, manganous water column conditions in intervals of Ediacaran successions that lack skeletal taxa (47).

The observations presented here support predictions as to the presence of diverse, pre-existing soft-bodied representatives prior to the acquisition of calcareous skeletons, and that the first macrobiota capable of first utilizing increased oxygen for extensive collagen fibrogenesis would likely be those with the lowest metabolic demands, in particular those without advanced circulatory-respiratory systems (46). It has been hypothesised that induced biologically-mediated calcification was an attempt to detoxify excess calcium ions (48), or the molecular inhibitors required as anti-calcification defences in soft-bodied ancestors might have been recruited for control over skeleton growth (34). It is possible that rising oxygen levels may, however, have been necessary to fuel the co-optive selection of proteins from a pre-adaptive state to allow an adaptive breakthrough (46).

Understanding the degree of biological control over Ediacaran macrobiota biomineralisation is critical. Biologically-induced precipitates form as a result of metabolic activities that affect pH, pCO_2, and secretion products where the cell is a causative agent only with no control over mineral type or habit (9, 49). By contrast, in biologically-controlled systems, cellular processes direct the nucleation, growth, morphology and final location of precipitated minerals. Almost all controlled mineralization processes occur in an isolated biological environment, although the degree of control varies considerably. A potentially widespread biomineralisation process also involves a transient amorphous calcium carbonate (ACC) precursor phase formed from a highly saturated solution with additions such as Mg or certain proteins that prevent crystallisation (49). Elemental compositional or microstructural heterogeneity is the mark of biologically-induced minerals, as the form biominerals resulting from induced processes vary according to the environmental settings in which they form (9,49). Analysis of individual crystal shapes and the stability of faces expressed can also inform the mechanisms of controlled growth, as can the nature of any biologically-controlled chemical and isotopic composition (vital effects).

Many, but not all, Ediacaran macrobiota skeletal microstructures are either microgranular or fibrous, with a non-hierarchical organisation. This perhaps suggests the operation of biomineralisation mechanisms that were not under tight biological control. Indeed we note that the

only biomineralised Ediacaran macrobiota to lack a non-mineralised twin possessed more advanced skeletal microstructures constructed of either multiple layers or several different fabrics, with a hierarchical organisation where each fabric has specific crystallites composed of sub-units similar to those known in earliest Cambrian skeletal metazoans (11). But a detailed understanding of Ediacaran biomineralisation processes is problematic, as evidence for environmentally-induced heterogeneity, the potential role of ACC, original crystal shape and preferred crystal orientation, and the presence of vital effects is difficult to establish given the diagenetic replacement of originally aragonitic or high Mg calcite skeletons and the unknown structure of the organic matrix.

A change in the ecological landscape further created by the rise of predation would have placed a premium on the acquisition of protective hardparts (1). The early Cambrian record shows a rapid increase in both diversity of mineralogy and complexity of skeletal microstructures which become conserved within lineages, suggesting that while calcification may first have arisen as a non-selective response to environmental change, it was later co-opted for defence and subsequently evolved under tighter biological control. Indeed we note also that skeletal hard parts first appeared in clastic environments in Cambrian Stage 1, suggesting independence from ambient sea water chemistry. By the early Cambrian genetic and molecular mechanisms may have controlled biomineralisation and mineralogy had become evolutionarily constrained (2).

7. Conclusions

We report that the oldest known skeletal macrobiota (ca.550 Ma), including unicellular eukaryotes and possible metazoans, found in carbonate settings, have almost morphologically identical soft-bodied counterparts often found in the clastic horizons of the same contemporary stratigraphic sequences. These forms are diverse, and include tubular and vase-shaped taxa, as well as the first example of a skeletonised discoidal fossil, possibly a holdfast, of Ediacaran Biota. In sum they represent problematic macrobiota, possible total group Cnidaria, as well as unicellular

eukaryotes. Skeletal microstructures are either microgranular or fibrous, with non-hierarchical organsiation.

We conclude that the macrobiota biomineralisation was first facilitated by the high carbonate saturation of Ediacaran seawater in local shallow, carbonate settings, and that such calcification was potentially under limited biological control in sessile taxa that probably required only modest modification of pre-existing organic templates.

The first appearance of large skeletal taxa may have been facilitated by changing seawater Mg/Ca and/or rise of oxygen. We hypothesise that from Ediacaran beginnings, macrobiota biomineralisation diversified in complexity and had become under tighter biological control by the early Cambrian, including occupation of clastic environments suggesting independence from ambient seawater chemistry, probably fuelled by an escalating defensive response to increasing predation pressure and other feedbacks.

Metazoans probably originated in the Cryogenian, diversified in the Neoproterozoic, and came to ecological dominance in the Cambrian. But molecular clock estimates predict the existence of only stem members of extant phyla in the late Ediacaran, with crown groups of most animal phyla originating in the Cambrian (50). Complex hierarchical Cambrian skeletal fabrics are notably different from the extremely thin, simple, Ediacaran skeletal organisations and represent a more advanced step in the evolution of biomineralisation.

Our findings support recent molecular evidence that the first appearance of fossil skeletons faithfully reflects their independent origins and further suggests that developmental and molecular architecture for biomineralisation evolved prior to the divergence of the metazoan phyla, providing a mechanism for synchronous, multiple origins of biomineralisation through exaptation of existing genes (2). This is also compatible with the assertion that the ‘Cambrian Explosion’ is a biological signal of the diversification of preservable skeletal fossils, not of animals.

Ethics statement

This work has not involved any living subjects and conforms to the Ethics guidelines of the School of GeoSciences, University of Edinburgh.

Data accessibility

All data utilised in this study are presented in the text.

Author contributions

RW and AZ designed the study; AI re-found the original *Suvorovella* fieldsite, undertook initial fieldwork, and collected most material. AI and AZ carried out the morphological description, undertook SEM analysis and reconstructed *Suvorovella*; RW undertook the petrographic analysis of *Suvorovella;* RW and AZ drafted the manuscript; All authors gave final approval for publication.

Competing interests

We have no competing interests

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Figure captions

Fig. 1. *Suvorovella aldanica* Vologdin and Maslov, 1960, Aim Formation, Ediacaran; Siberian Platform, Republic of Sakha (Yakutia), Russia. (A) Detail of shell inner lower surface showing outer flat zone with diamond-shaped pattern and concentrically arranged chambers. **(B)** Detail of shell showing folded apex and outer flat zone with diamond-shaped pattern, latex mould of inner lower surface, PIN no. 5119/1063. **(C)** Reconstruction, diameter 100 mm. **(D)** Field photograph of shell bed of whole and broken *Suvorovella* shells. **(E)** Photomicrograph of thin section showing micritic envelopes (arrowed) around *Suvorovella*, encrusted by an isopachous crust of early diagenetic radial fibrous dolomite cement. **(F)** SEM image of detail of outer upper surface of shell at the apex showing concentric ribs and uneven surface. **(G)** SEM image of broken shell edge showing micrite envelope (M) encrusted by early marine radial fibrous dolomite cement (D). Specimens figured in A, B, F and G are housed in Palaeontological Institute named after A.A. Borisyak, Russian Academy of Sciences, Moscow (PIN).

Fig. 2. Ediacaran skeletal (A-D) and non-skeletal (E-H) counterparts. (A) Skeletal *Suvorovella*;. **(B)** Skeletal *Cloudina* (Photo: Shuhai Xiao). **(C)** Skeletal *Sinotubulites* (Photo: Shuhai Xiao/Yaoping Cai). **(D)** Skeletal *Protolagena* (Photo: Shuhai Xiao/Hong Hua). **(E)** Organic *Eoporpita medusa*. **(F)** Organic *Conotubus* (photo: James Schiffbauer/Yaoping Cai). **(G)** Organic *Corumbella* (photo: Lucas Warren). **(H)** Organic *Sicylagena* (Photo: Shuhai Xiao/Hong Hua).

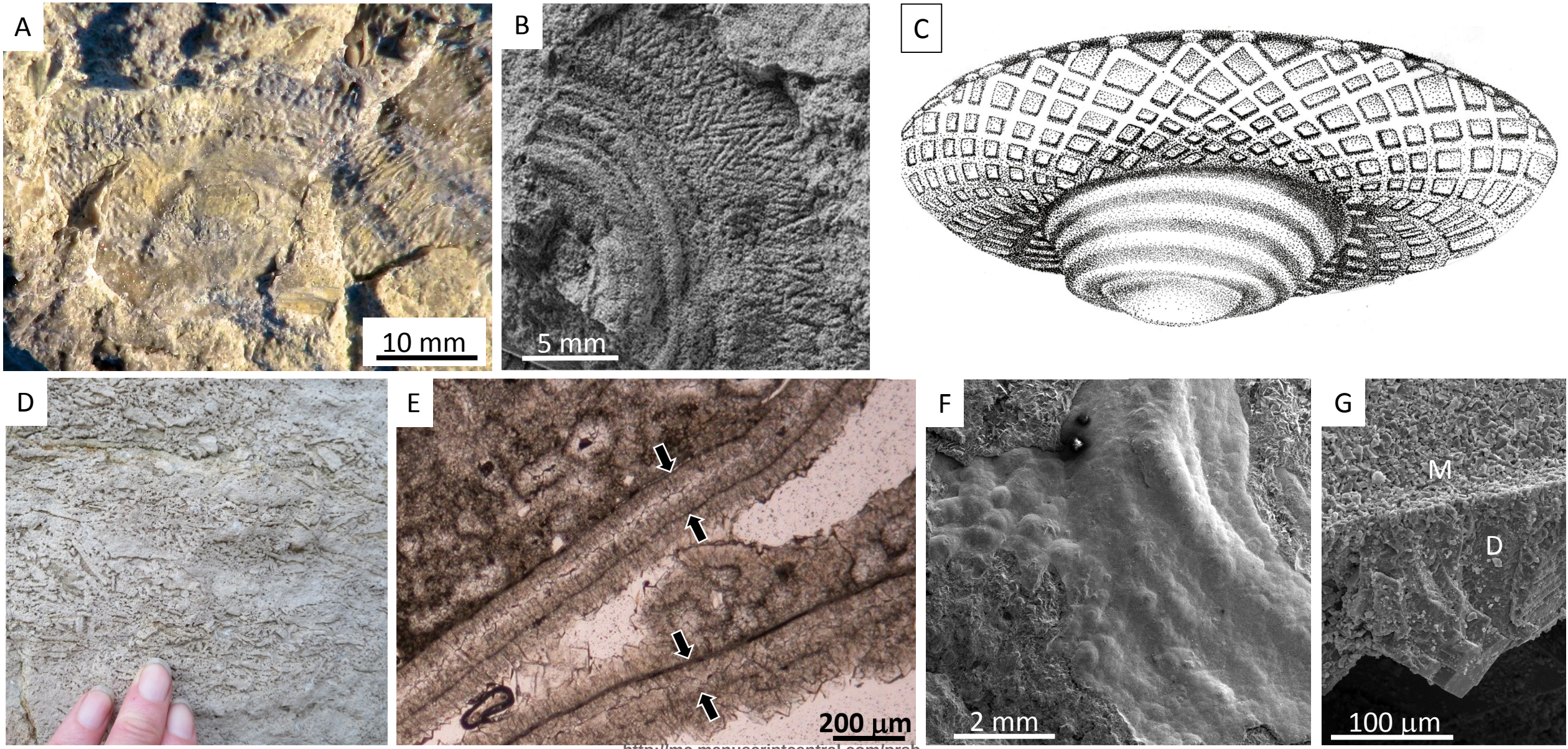

Figure 1

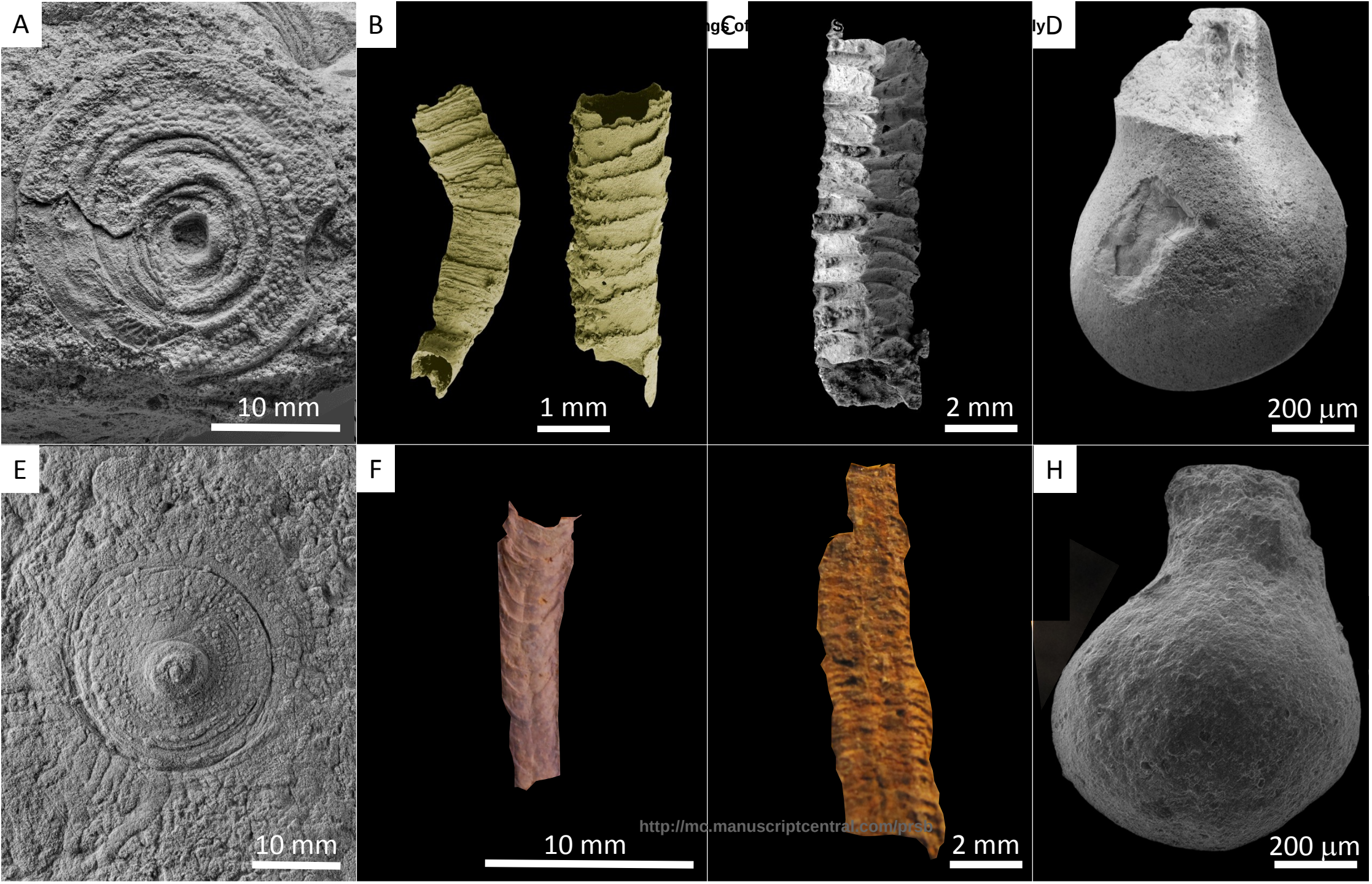

Figure 2